

THE FEEDING TECHNIQUES OF STILT SANDPIPERS AND DOWITCHERS

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ABSTRACT.—This paper presents descriptive and quantitative observations of feeding behavior of Stilt Sandpipers (*Micropalama himantopus*) and dowitchers (*Limnodromus* spp.). Stilt Sandpipers make frequent use of “stitching”—a series of extremely rapid jabs into the mud surface, performed while pivoting the body or walking. This is probably a means of tactile foraging; visual searching behavior is also used. Dowitchers do not “stitch” but employ isolated (though frequent) deep jabs and probes, which are often prolonged and vigorous. They show little evidence of hunting by sight. The differences provide further evidence for assigning the Stilt Sandpiper and dowitchers to the Calidridinae and Scolopacinae, respectively. Significant differences in anatomy of the feeding apparatus are summarized.

The great diversity in bill shape and size among shorebirds leads one to expect a corresponding diversity in feeding techniques and methods; yet there have been few really detailed and quantitative studies of these techniques. One of the most thorough, concerning European shorebirds, is a little known study by Streefkerk (1960). Detailed descriptions of feeding methods in five species of shorebirds, with a summary of information available for others, are given by Burton (1969, and in press). The present paper concerns dowitchers (*Limnodromus* spp.) and the Stilt Sandpiper (*Micropalama himantopus*). Various descriptions in the literature suggest a close similarity between the feeding methods of these birds, and both are often stated to employ a “sewing-machine action” (e.g., by Peterson, 1947). The best accounts are those of Bent (1927) and Palmer (1967), but these include observations from a variety of sources and are insufficiently detailed for comparative purposes.

Dowitchers and Stilt Sandpipers have often been considered closely related, as indicated by their juxtaposition in many North American lists until recently. According to an alternative view (Lowe, 1931; Peters, 1934) the Stilt Sandpiper is closely related to *Calidris* (Scolopacidae, subfamily Calidridinae), while dowitchers are allied to the snipes, *Gallinago* spp. (subfamily Scolopacinae). This view is reinforced by recent work (Jehl, 1968; Burton, in press). As the Calidridinae and Scolopacinae differ extensively in feeding methods, the alleged similarity in this respect between dowitchers and the Stilt Sandpiper is surprising. Therefore, during the course of a visit to Texas during the latter half of April, 1969, I took the opportunity to make detailed observations on their feeding behavior.

METHODS

Stilt Sandpipers were watched principally at a brackish pool lying between agricultural land and mesquite brush near Alamo, lower Rio Grande valley, Texas. Dowitchers (mostly *L. griseus*) were watched at tidal pools on the mudflats of the west (Laguna Atascosa) shore of Padre Island, near Port Isabel, Texas. Observation was by telescope (30× to 60×). Quantitative aspects were studied by dictating running commentaries into a portable tape recorder. This provided data amenable to statistical treatment, and to timing of various items; some timed data were also obtained in the field, using a stop watch. Prolonged examination of qualitative aspects of behavior were also made, in addition to the taped recorded commentaries. The total observation time (about 20 hours for each species) is relatively brief but served to clarify considerably the similarities and differences between the two species in feeding methods.

STILT SANDPIPER

Three principal types of feeding action were distinguished:

- a. *Pecks.*—These are extremely brief movements made into water, or at its surface, or

into the surface of exposed mud.

- b. *Probes*.—Longer movements in which the bill is thrust into the mud for some depth. As in the case of Dunlin (*Calidris alpina*) studied by Burton (in press), these are normally made with a very rapid up-and-down quivering action. This, and their distinctly longer duration, are the only means of distinguishing them from pecks when (as frequently happens) the insertion of the bill into the mud cannot be seen.
- c. *Stitching*.—This term is used by Burton (in press) to refer to a feeding action which appears to be characteristic of the Calidridinae. It has previously been described from several members of the subfamily by Streefkerk (1960), Holmes (1966), and others. Basically, stitching consists of very rapid series of shallow jabs into the mud surface, made while on the move; Holmes (1966) refers to it simply as a “rapid series of jabs.” Stitching and probes may appear closely similar, and in fact intergrade; probes are generally made in one spot, and usually deeper and more vigorously than stitching.

The Stilt Sandpipers invariably fed on mud covered by a layer of water, sometimes barely covering the feet, but usually to about tarsus length, and commonly to belly depth. A notable characteristic mentioned by several authors is their lack of mobility. This is especially striking by comparison with other species feeding near them in similar situations, in this case Lesser Yellowlegs (*Tringa flavipes*) and Wilson's Phalarope (*Phalaropus tricolor*). This lack of mobility is also a contrast to most other members of the Calidridinae, which, however, generally feed in shallower water or on exposed substrates.

Several accounts of the habits of the Stilt Sandpiper mentioned a characteristic attitude, with neck outstretched and bill pointed vertically down. This attitude is indeed well marked in this species, though a similar attitude is quite often assumed by other shorebirds (e.g. Redshank, *Tringa totanus*) wading in fairly deep water. It is restricted to spells of feeding by means of pecks; stitching series are carried out with the bill inclined at about 80° to the horizontal, as in other Calidridinae. The more perpendicular bill carriage where pecks predominate is probably related to the fact that these are used in hunting by sight; the perpendicular attitude may serve to minimize errors due to refraction. Stitching, on the other hand, appears to be a form of trial probing with the object of detecting prey by tactile means. The behavior of the birds while making pecks gave a strong impression that they were engaged in visual search. They would walk slowly about, on a zig-zag path or backwards and forwards, not covering a great amount of ground, but maintaining the outstretched neck and perpendicular attitude throughout.

Stitching usually involves even less mobility, and one bird may spend an hour or more in an area only a yard or so across; similar lethargy mentioned by Bent (1927) and Palmer (1967) probably refers to birds feeding in this way. By contrast with most *Calidris* species, which usually stitch while walking, Stilt Sandpipers generally carry this out while standing still, the only movement usually being a side to side pivoting at the pelvis combined with neck action, so that the stitching jabs are made around it in a semicircle. The tracks left by this process should have been highly characteristic if there were any, but the mud surface was much too soft to retain indentations. The bird seen swinging its immersed bill from side to side mentioned by Bent and Palmer was very probably stitching. Palmer's comparison with a side to side action seen in the Greater Yellowlegs (*Tringa melanoleuca*) is probably misleading. A side to side action is shown by a variety of Tringinae, especially Redshank (*T. totanus*) and Willet (*Catoptrophorus semipalmatus*), but close examination shows it to be accompanied by very rapid opening and shutting jaw movements, a feature never seen in the stitching of Calidridinae which it superficially resembles.

Stitching was usually performed in more shallow water than feeding by pecks, though some prolonged spells of stitching took place with the head completely immersed, only the quivering and slow pivoting of the body indicating what was happening. On the rare occasions when stitching was carried out on virtually exposed mud, it could be seen that the bill was very slightly open at the tip, as in Dunlin. The duration of 321 stitching sequences timed gave a mean of 2.3 secs with a maximum of 13.7 secs. This is somewhat shorter than that recorded for Dunlin (mean 3.9, maximum 25.7) on a tidal mudflat by Burton (in press) though it is pointless to pursue the comparison too closely.

Probes were relatively brief, the great majority lasting under one second. Since most

were made under water (usually of belly depth), the depth to which the bill was inserted into the mud could not normally be seen; when visible, the amount of insertion appeared not less than half the bill length, and frequently its full length. No changes of bill orientation were seen during the course of a probe. The great majority of probes were isolated, but up to six have been observed in one spot, presumably in efforts to capture a particularly difficult prey animal. Most obvious captures (indicated by head jerking and swallowing movements) followed probes rather than pecks; probably the items acquired by pecking were mostly so small that their capture went unobserved.

The proportions of pecks, probes and stitching sequences in 52 minutes of timed observations were recorded (Table 1). Each stitching sequence was counted as a single movement. The mean number of feeding movements per minute was 40.2 (min. 10, max. 82). High rates were associated with a large proportion of pecks—not surprisingly, since pecks are the most rapid movements. Conversely, low rates are associated with a high proportion of spells of stitching, which are of longer duration than pecks or probes. Interestingly, highest probing rates occur around the middle of the range of total frequencies, and relatively few probes followed stitching sequences, contrasting with the Dunlin studied previously (Burton, in press). Evidently visual signs provided the clues leading to a probe in the majority of cases. Stitching thus appeared a relatively inefficient method of locating prey in this area, though it may have been more important near the edges of the pool, where prey were possibly deeper lying. In other situations, and especially at night, it may well be of much greater value.

Table 1. Summary of timed observations on feeding movements of individual Stilt Sandpipers.

Rate (Total movements per minute)	Number of minutes	Combined totals	Stitching	Pecks	Probes
10 to 19	5	79	77	2	0
20 to 29	8	192	123	32	37
30 to 39	14	483	8	197	278
40 to 49	13	598	19	273	306
50 to 59	6	317	34	269	14
60 to 69	3	190	3	151	36
70 to 79	2	145	6	126	13
80 to 89	1	82	0	44	38
Overall total	52	2086	270 (12.9%)	1094 (52.4%)	722 (34.5%)

DOWITCHER

Only two types of feeding action could be distinguished:

- Jabs*.—These are simple, brief movements in which the bill is thrust into the mud and immediately withdrawn.
- Probes*.—More prolonged movements in which the bill is thrust into the mud and held there for a short time, usually accompanied by a rapid up-and-down quivering action.

Probes are generally deeper than jabs, mostly between one third and the full length of the bill (where depth of insertion could be clearly seen), whereas most jabs were to less than half the bill length. However, the main distinction was the brevity of jabs, which were generally too rapid for accurate timing, though apparently under 0.5 seconds in duration. 103 probes timed averaged 1.7 seconds, with maxima of 4.1 and 7.3 seconds.

This classification is to some extent arbitrary, but probably most jabs are trials made in searching for prey by tactile means, while probes include most of the actions in which prey are actually captured. Probes were often grouped in one place. When this was the case, they were often made with obvious vigor, and frequently with the capture of a prey animal, as indicated by swallowing movements. Presumably, in such cases, prey had been located, but

several attempts were needed to complete its extraction.

The dowitchers were nearly all feeding in tidal pools, frequently up to belly depth; a few were watched feeding on exposed mud. Though none ever showed the remarkable attachment to one spot displayed by some Stilt Sandpipers, their mobility was not great. Most commonly, a bird would concentrate on a small area for about 30 seconds, probing around itself with pivoting movements of the body and a leisurely step or two; then walk on more briskly for a few seconds, and pause to repeat the process. Long series of jabs were sometimes made while walking steadily forwards; however, these could not be confused with the stitching of Stilt Sandpipers and *Calidris* spp., as the frequency of jabs was far less rapid, and the bill was raised well clear of the mud between each.

Rates of feeding movements were generally high. The mean rate during 61 minutes of timed observations (Table 2) was 60.6 (min. 36, max. 110). Not surprisingly, high rates coincided with high proportions of jabs. Overall, there were slightly less (48%) jabs than probes. Highest rates were recorded from birds feeding on exposed mud, which employed a high proportion of jabs, and apparently met with little success. Birds feeding in this situation were occasionally seen to make short runs and sudden turns, suggesting pursuit of prey located by sight.

Between feeding actions, dowitchers held the bill inclined at about 70° or 80° to the horizontal. An attitude with neck outstretched and bill pointed vertically down, as in Stilt Sandpiper was never seen. The orientation of the bill was rarely altered to any significant extent during the course of a probe, though on one occasion the bird turned a full circle around its bill during a single probe. The probes themselves were sometimes made with considerable force and vigor, quite unlike anything seen in the Stilt Sandpiper.

No prey item was at any time seen. Several samples of mud in areas favored by dowitchers were dug up and carefully sifted, but the only animal species found was the small (5 to 9 mm.) bivalve *Lyonsia hyalina* Conrad. This mollusk is evidently abundant in the area, and may well have been the main prey of the dowitchers observed.

Table 2. Summary of timed observations on feeding movements of individual dowitchers.

Rate (Total movements per minute)	Number of minutes	Combined totals	Jabs	Probes
30 to 39	2	74	10	64
40 to 49	8	359	96	263
50 to 59	20	1099	455	644
60 to 69	18	1164	591	573
70 to 79	10	726	402	324
80 to 89	2	162	117	45
110	1	110	93	17
Overall total	61	3694	1764 (47.8%)	1930 (52.2%)

COMPARISON

Dowitchers and Stilt Sandpipers certainly show some similarities while feeding. Both forage largely in pools and show a generally high rate of feeding movements combined with low mobility. Their feeding actions are mostly simple, fairly regular movements, made more or less straight downwards. The impression of similarity is heightened by contrast with other waders feeding in the same situations, notably Greater and Lesser Yellowlegs, whose brisk actions include dashes and sudden turns.

Nevertheless, there are well marked and important differences. The most obvious of these is the absence of "stitching" in Dowitchers—notwithstanding the fact that the actions of both birds have been likened with some justice to a sewing machine. Despite the similarity of imagery, it must be remembered that the term "stitching" as used here and else-

where (Burton 1971, and in press) applies specifically to an extremely rapid series of shallow jabs, made with minimum head movement. This action, seen in many calidridine sandpipers, including the Stilt Sandpiper, was never observed from dowitchers during the course of these observations. Conversely, Stilt Sandpipers rarely used deep test probes, whereas the jabs of dowitchers regularly penetrate to a third or more of their considerable bill length. Probes in both species are made with a similar quivering action, but Stilt Sandpipers never exhibit the vigor and forcefulness which is often shown by probing Dowitchers.

The attitude with neck outstretched and bill pointed perpendicularly down is characteristic of Stilt Sandpipers but is rarely shown by Dowitchers. As explained earlier, this attitude is probably connected with hunting by sight, and indicates the much greater importance of vision for feeding in the Stilt Sandpiper—a factor which underlies other differences between their feeding techniques. Stitching as a means of tactile foraging increases the chances of contact with prey lying near the surface in a given time, but must be relatively inefficient for detecting deeper lying prey. The individual jabs in a stitching series are shallow, and probably only penetrate the soft surface layer of water covered mud; they require relatively little anatomical specialization, and form part of a generally more versatile range of feeding techniques. The generally deeper jabs of dowitchers stand a greater chance of detecting deep lying prey, but there are many fewer in a given time. Also, since the head is fully raised and lowered between each one, and the deeper penetration involves entering a harder substrate, the amount of energy expended in proportion to the number of contacts with prey may well be greater in dowitchers. This is probably offset to some extent by greater tactile sensitivity in dowitchers. Moreover, dowitchers are capable of handling considerably larger prey than Stilt Sandpipers, and since these tend to be deeper lying dowitchers may be expected to encounter more of them. The feeding technique and anatomy of dowitchers thus probably depends on relatively infrequent contacts with larger prey.

Detailed information on anatomy of the feeding apparatus in shorebirds is given by Kozlova (1961-62) and Burton (in press). The points of difference between dowitchers and Stilt Sandpipers summarized below appear particularly relevant to a comparison of feeding methods.

- a. The bill axis is considerably more downwardly directed relative to the cranium in dowitchers.
- b. The dorsal bar of the upper jaw is greatly reinforced in dowitchers, and is almost in contact with the ventral bar. In the Stilt Sandpiper, both ventral and dorsal bars are thin and widely separated.
- c. Hexagonal pits, indicating clusters of tactile receptors (Herbst's corpuscles) are much more numerous at the tips of the jaws in dowitchers.
- d. *M. protractor quadrati*, which raises the tip of the upper jaw, is enormous in dowitchers by comparison with the Stilt Sandpiper.
- e. *M. adductor externus* (of major importance for jaw closure and gripping prey) is relatively larger in dowitchers, and of more complex structure, with more pinnate fiber arrangements—a modification to increase the force of contraction over short distances.
- f. *M. rectus capitis superior*, a flexor of the head and anterior part of the neck, lacks attachment to vertebra 4 in the Stilt Sandpiper. This curious feature, unique among shorebirds, is probably connected with its characteristic head attitude with bill pointed straight down, while feeding in water.

In most of these, and other anatomical features of head and neck, the Stilt Sandpiper is typical of the Calidridinae, whereas dowitchers closely approach the Scolopacinae, though showing some similarity to members of the Tringinae. Dowitchers have by some authors (e.g., Kozlova, 1961-2) been considered more closely allied to godwits, but Jehl (1968) has produced strong evidence for their close relationship to the Scolopacinae, first proposed by Lowe (1931). The results of this study bear out Jehl's view. The feeding technique of dowitchers closely resembles that of Snipe (*Gallinago gallinago*), described in detail by Burton (in press), in the great reliance of both on simple probing, and in the manner, timing, and disposition of probes. They certainly show little resemblance to the versatile techniques of the much more mobile godwits. Similarly, the feeding behavior of Stilt Sandpipers, with its frequent use of "stitching" is very similar to that of other Calidridinae, though with modifi-

cations for feeding in deeper water than most of the subfamily.

In any further study of feeding in dowitchers and Stilt Sandpipers, it would be desirable to observe them in an area where both forage together. I saw them in close proximity on various stretches of shore in the Laguna Atascosa Refuge, but was not able to prolong my observations there. Such a comparison might throw further light on the results obtained by Recher (1966) in a comparison of waders sharing a stretch of shore. It would be particularly interesting to know whether dowitchers (the larger species) take a narrower spectrum of prey, including more large items, than the Stilt Sandpiper. Such a difference might be expected from Recher's analysis of diets in relation to body size, though in the experience of Jehl (pers.comm.) the reverse seems to be the case at Churchill, Manitoba, where the two species often feed in close proximity.

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LITERATURE CITED

- Bent, A. C.
1927. Life histories of North American Shore Birds. Part I. U.S. Natl. Mus. Bull. 146.
- Burton, P. J. K.
1969. Anatomy and adaptive modifications of the feeding apparatus in waders (Aves: Charadrii). Ph.D. thesis, University of London.
1971. Comparative anatomy of head and neck in the Spoon-billed sandpiper, *Eurynorhynchus pygmeus* and its allies. J. Zool., Lond., 163: 145-163.
In press. Feeding and the feeding apparatus in waders. British Museum (Natural History).
- Holmes, R. T.
1966. Feeding ecology of the Red-Backed Sandpiper (*Calidris alpina*) in Arctic Alaska. Ecology, 47: 32-45.
- Jehl, J. R., Jr.
1968. Relationships in the Charadrii (shorebirds): a taxonomic study based on color patterns of the downy young. San Diego Soc. Nat. Hist., Memoir 3.
- Kozlova, E. V.
1961-1962. Fauna S. S. S. R., Zool. Inst. Akad. Nauk S. S. S. R., nov. ser. no. 81, Ptitsy, 2, no. 1, pt. 3 [Birds, Charadriiformes. Suborder Limicolae] Moscow-Leningrad. Akad. Nauk. S. S. S. R.
- Lowe, P. R.
1931. An anatomical review of the "waders" (Telmatomorphae). Ibis, 1931: 721-771.
- Palmer, R. S.
1967. Species accounts, In G. D. Stout (ed.), The Shorebirds of North America. Viking Press, New York.
- Peters, J. L.
1934. Check-list of birds of the world. Vol. 2. Harvard Univ. Press, Cambridge.
- Peterson, R. T.
1947. A Field Guide to the Birds. Houghton-Mifflin Co., Boston.
- Recher, H. F.
1966. Some aspects of the ecology of migrant shorebirds. Ecology 47: 393-407.
- Streefkerk, C. J.
1960. Verslag van het vergelijkend onderzoek naar de wijze van voedsel zoeken van enige soorten steltlopers. Uitgegeven door de Christelijke Jeugdbond van Natuurvrienden, Amsterdam.

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